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## PALEOCLIMATIC INFERENCE FROM MORPHOLOGICAL STRUCTURE IN THE SNAIL *GASTROCOPTA PROCERA* (GASTROPODA: PUPILLIDAE)

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### ABSTRACT

This study describes relationships between morphometric parameters of Cenozoic populations of *Gastrocopta procera* (Gould, 1840) and climatic variables for the north central United States over which the snail is currently distributed. We use the multivariate techniques of principal components analysis and multiple linear regression to illustrate how the response of snail structure to climatic variation in extant populations can be used to predict climatic conditions for fossil populations. Five Pliocene populations of *G. franzenae* Taylor, 1960, two Holocene populations of *G. riograndensis* (Pilsbry and Vanatta, 1900) and one of *G. cristata* (Pilsbry and Vanatta, 1900) also were studied. Four climatic variables (latitude, longitude, total annual precipitation, and number of frost-free days) have a highly significant predictive value for the major axis of morphological variation in extant populations of *G. procera*. This axis accounts for more than half of the structural variation among 339 specimens sampled from 31 extant populations across the biogeographic range of the species. Extrapolation of relationships between morphological structure and modern climatic conditions to fossil populations strongly suggests that the populations represented by fossils lived in conditions similar to those now present in the southern parts of the range of *G. procera*. These analyses imply that populations of the putative ancestral species, *G. franzenae*, may have lived under conditions warmer and wetter than those of present-day populations of the descendant species.

### Introduction

The primary purpose of this paper is to demonstrate relationships between morphometric parameters of populations of a snail and climatic variables for the continental region over which the snail is distributed. We illustrate how the response of snail structure to climate in extant populations can be used to predict climatic conditions for fossil populations of this snail.

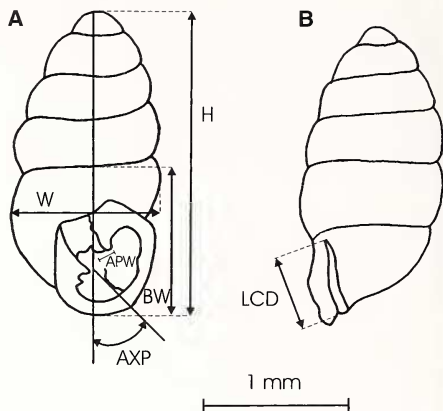
Paleoclimatic reconstructions using nonmarine molluscs typically assume that climate is a major factor controlling their distributions (Hibbard and Taylor, 1960, p. 16–19; Taylor, 1960, p. 4–9; Sparks, 1961; Lozek, 1964, p. 49–53; Harris and Pip, 1973; Baerreis, 1980; Miller and Kay, 1981; Keen, 1990). Only rarely have these assumptions been subjected to quantitative analysis. We are aware of only one such study in North America, involving the terrestrial pulmonate gastropod, *Gastrocopta procera* (Gould, 1840), a statistical analysis which suggested that some of the variation in shell morphology appeared to be related to climatic variables (Couri, 1976).

*Gastrocopta procera* and the closely related species *G. cristata* (Pilsbry and Vanatta, 1900) are extant species with relatively broad distributions in the eastern United States (Pilsbry, 1948, p. 907, p. 913; Hubricht, 1985, p. 72). They are also common as fossils in many of the Pleistocene molluscan faunas reported from the southern Great Plains (Hibbard and Taylor, 1960, p. 10; Taylor, 1965, p. 607; Miller, 1976). Another common Holocene species, *G. riograndensis* (Pilsbry and Vanatta, 1900, p. 595), is also morphologically similar to *G. procera*.

Some of the morphological shell characters that distinguish *G. procera* and *G. cristata* from each other have been found occurring together in many individuals from several different Pliocene fossil localities. Taylor (1960, p. 67–69) considered the morphological overlap in these Pliocene shells to justify a new species, *G. franzenae*, and suggested that *G. franzenae* was the probable ancestral species that evolved into *G. procera* and *G. cristata* during the Pleistocene. If true, this would be one of the few known examples documenting the evolution of a new terrestrial pulmonate snail species during the Pleistocene.

Our investigation started as a study of the nature and magnitude of the evolutionary changes in shell morphology that could be measured in the fossil shells of *G. procera* from the Pleistocene faunas of the southern Great Plains (Couri, 1976). *Gastrocopta procera* was chosen for study because its shell characteristics permitted unequivocal identification to species (Figure 1) and the availability of both modern and fossil materials for study in museum collections.

The range of shell variation was evaluated in recent populations of *G. procera* from 14 localities over much of its modern range in the continental United States. Measurements were made of the several aspects of shell



**Figure 1.** Diagram of a *Gastrocopta procera* specimen showing the primary morphometric landmarks and variables. A, ventral view; B, lateral view. Abbreviations and definitions of parameters are given in Table 2.

morphology that have been used to distinguish various members of this cluster of species. Preliminary results from this phase of the study yielded statistically significant correlations between particular morphological measurements with certain climatic parameters, such as temperature and precipitation, for the collection sites (Couri, 1976). The potential usefulness of these shell-climate interrelationships for paleoenvironmental reconstructions led to an expansion of this study into the current report.

### Materials and Methods

Samples from Holocene populations of the snail *Gastrocopta procera* were obtained from 31 localities across the current geographic range of the species (Table 1); a total of 614 specimens were used in various analyses. Museum lots were selected for which there was reasonable certainty that the specimens were collected alive and at their living site. Thus, stream drift material, although abundant in museum collections, was excluded. In addition to these representatives of *Gastrocopta procera*, samples were obtained of five Pliocene populations of *G. franzenae* (a total of 141 specimens), two Holocene populations of *G. riograndensis* (37 specimens), and one Holocene population of *G. cristata* (29 specimens).

All specimens were cleaned and body remnants removed by soaking in 50 percent household bleach solution, using ultrasonic agitation as necessary. Only mature specimens, as judged by the presence of lamellae within

**Table 1.** Sampling localities, codes, and sample sizes. Samples A through AE represent populations of *Gastrocopta procer*a; samples 1–5 are of *G. franc*enae; samples r and g belong to *G. riograndensis*; and sample c belongs to *G. cristata*. Museum abbreviations are as follows: KSU, Kent State University, Department of Geology; MCZ, Museum of Comparative Zoology, Harvard University; UMMZ, University of Michigan Museum of Zoology.

Code	Sample size	Museum lot no.	Geographic location	Lat. (N)	Long. (W)
A	22	UMMZ 106898	Orange Co. VA	38° 15.6'	77° 59.8'
B	30	MCZ 54573	Dallsville MD	38° 34.2'	76° 04.7'
C	13	MCZ 95876 & MCZ 46852	Knoxville TN	35° 58.1'	83° 55.1'
D	30	MCZ 3851 & UMMZ 106894	Cincinnati OH	39° 06.0'	84° 30.8'
E	21	MCZ 9659	Albion IL	38° 22.6'	88° 03.5'
F	24	MCZ 94679	St. Louis Co. MO	38° 37.0'	90° 11.6'
G	12	UMMZ 106905	Calceira AL	33° 16.4'	86° 42.5'
H	7	UMMZ 106955	Trego Co. KS	38° 54.6'	99° 52.8'
I	18	KSU 1970	Ellis Co. KS	38° 54.6'	99° 19.5'
J	26	KSU 7460	Beaver Co. OK	36° 43.7'	100° 31.3'
K	12	UMMZ 106928	Weicher Co. OK	36° 43.7'	100° 31.3'
L	30	UMMZ 106932	Wichita Mtns OK	34° 51.0'	98° 27.8'
M	30	UMMZ 106926	Dundee TX	33° 35.7'	98° 41.5'
N	30	UMMZ 165464	Comfort TX	29° 57.0'	98° 39.8'
O	11	MCZ 98221	Bear Creek AL	32° 20.3'	87° 12.1'
P	30	MCZ 3849	Washington DC	38° 53.5'	77° 02.0'
Q	24	USNM 474086	Yorktown VA	37° 14.1'	76° 30.4'
R	24	USNM 448536	Wilmington NC	34° 14.2'	77° 55.4'
S	16	USNM 68744	Nashville TN	36° 09.8'	86° 46.7'
T	13	USNM 231926	Kansas City MO	39° 06.0'	94° 34.7'
U	24	USNM 416301	Lincoln NB	40° 49.4'	96° 41.1'
V	15	USNM 424002	Topeka KS	39° 03.1'	95° 40.2'
W	24	USNM 520233	Sayre OK	35° 17.7'	99° 38.4'
X	8	USNM 536571	Colman TX	31° 44.5'	99° 29.1'
Y	24	USNM 448585	Amarillo TX	35° 12.5'	101° 50.0'
Z	11	USNM 102555	Lee TX	30° 17.1'	96° 57.7'
AA	12	USNM 511718	Lee TX	30° 17.1'	96° 57.7'
AB	24	USNM 106948	Grant LA	31° 34.7'	92° 31.1'
AC	13	USNM 473858	Colbert AL	34° 43.9'	87° 49.0'
AD	12	USNM 448594	Mobile AL	30° 41.3'	88° 02.6'
AE	24	USNM 511230	Indianapolis IN	39° 46.2'	86° 09.3'
1	30	UMMZ 183033	Meade Co. KS	37° 00.7'	100° 32.0'
2	30	KSU 0046	Meade Co. KS	37° 00.7'	100° 32.0'
3	21	UMMZ 183001	Oldham Co. TX	35° 34.8'	102° 29.3'
4	30	UMMZ 184153	Seward Co. KS	37° 03.0'	100° 55.8'
5	30	UMMZ 183068	Meade Co. KS	37° 14.4'	100° 21.6'
r	14	UMMZ 106957	Valles MX	21° 15.0'	99° 26.0'
g	23	UMMZ 34269	Brownsville TX	25° 54.0'	97° 30.0'
c	29	KSU 7461	Sayre OK	35° 17.6'	99° 39.1'

**Table 2.** Morphometric parameters, climatic variables, and their abbreviations.

Variable	Unit	Description
H	mm	height of shell, from apex to reflected peristome, along columellar axis
W	mm	width of shell, measured perpendicular to the body axis
WL	count	number of whorls, to nearest quarter-revolution
APW	mm	maximum angulo-parietal lamellar width
AXP	°	angle between columellar axis and axis of lower palatal lamella
LCD	mm	lip-crest distance, from aperture lip edge to crest axis
BW	mm	height of body whorl, from outer edge of reflected peristome to suture between body whorl and second whorl
LAT	°N	latitude
LONG	°W	longitude
FROST	inches	average depth of frost penetration
TEMPAVE	°F	average annual temperature
TEMPPL	°F	average July temperature
PRECSUM	inches	average summer precipitation
PRECAVE	inches	average annual precipitation
FFREE	days	average number of frost-free days
LASTKILL	date	average day of last killing frost in Spring
FIRSTKILL	date	average day of first killing frost in Fall
CLOUDY	days	average number of cloudy days per year

the aperture and the crest on the external labium, were used. Cleaned, mature specimens were mounted in 60-division faunal slides with gum-tragacanth solution. Using a Gaertner coordinate microscope (with “flat” optics), specimens were mounted with the aperture up and the rim of the peristome as horizontal as possible.

Morphometric data for all specimens were collected by a single observer using a Gaertner coordinate micrometer. Figure 1 illustrates key structural features of this snail used to define the corresponding morphometric variables. Table 2 gives the list of measurements and their abbreviations; however, three parameters (APW, LCD, and BW) were not measured for all of the populations, as noted in subsequent tables. In order to measure LCD, specimens were rotated 90° clockwise and remounted with the aperture to the left and the aperture rim vertical (as shown in Figure 1B).

Shell height (H) was measured by a traverse along the columellar axis from the apex to the outer edge of the reflected peristome, while the height of the body whorl (BW) was measured by traversing the same axis in the reverse direction until the crosshairs rested on the suture between the body whorl and the second whorl. The shell width (W) was measured by a traverse across the body whorl perpendicular to the body axis. Angulo-parietal width (APW) was measured by traversing across the tuber-

cle. The angular measurement (AXP) was obtained by positioning the vertical crosshair on the columellar axis with the origin overlying the columellar denticle, and then rotating the stage until the lower palatal lamella was parallel to the vertical crosshair. The lip-crest distance (LCD) was obtained by traversing the remounted specimen at right angles to the axis of the crest.

Climatic data for the sample localities were taken from the nearest reporting station of the United States Weather Bureau, for the period 1899–1938. The nine climatic parameters that were used correspond to average values for the nearest station, determined from published maps (Kincer, 1941). Their descriptions and abbreviations are given in Table 2. We inspected the relationship between each of the original morphometric parameters for the extant populations and the climatic variables corresponding to their sample localities by means of bivariate linear regression. However, only the two highest correlations are reported.

All statistical analyses were performed using the S-PLUS 2000 software package (MathSoft, 1999). Two primary analytical techniques were used. To examine the main dimensions of the multivariate structure of the morphometric data, for both extant and fossil populations, we used principal components analysis (Morrison, 1967; Gauch, 1982). This technique constructs linear combinations of the original measurements that maximally encompass the multivariate variation in the data. In particular, the first principal component accounts for the greatest variation in the data; the second component is orthogonal to the first component (i.e., is perpendicular to it and uncorrelated with it) and accounts for the second largest amount of variation; the third component is orthogonal to the first two and accounts for the next largest amount of variation; etc. The principal components provide a mathematically unique solution that effectively reduces the dimensionality of the original data. Typically, instead of having a large number of correlated measurements that together describe the morphological structure of an organism, the first few principal components often are sufficient to encompass most of the variation among the individuals in the several sampled populations. These synthetic variables thus represent uncorrelated aspects of organismal structure. Because two of the original morphological variables represented angular measurements, while the others were linear measures of the size of various aspects of the shell, our principal components analyses were based on the correlation matrix among the variables.

The principal components for the morphological structure of *G. procera* then were related to latitude, longitude, and the nine more specific climatic variables for the sample locations by using multiple linear regression techniques (Gauch, 1982; Sokal and Rohlf, 1995). Another

principal components analysis was undertaken with all four species, in order to examine possible changes in morphological structure over time. The final step in the analysis was to use the interpretation of the morphological principal component axes in terms of climate (via regression) to predict possible climatic conditions for the fossil populations on the basis of their physical structure, as indicated by their location in principal component space.

## Results and Discussion

### Univariate and bivariate analyses of extant populations

Table 3 presents the mean values for each measurement at each of the 31 sample localities of *G. procera*, as well as the mean annual values of each of the climatic variables at the nearest recording station. To investigate possible relationships between extant morphology and modern climatic conditions, we calculated the matrix of bivariate correlation coefficients, based on these mean values, between each of the seven structural parameters and each of the 11 climatic variables (Table 4). Linear regression analyses were performed on each of the 61 statistically significant correlations after correction for multiple comparisons (Sokal and Rohlf, 1995). However, because our primary focus is the relationship between the totality of morphological structure, which is a multivariate phenomenon, and possible climatic influences, here we present only the results of the two most significant bivariate correlations, viz., that between AXP and latitude ( $r = 0.843$ ,  $P < 0.001$ ) and that between LCD and latitude ( $r = -0.819$ ,  $P < 0.001$ ). Figure 2 shows the strong linear relationship between the mean values for the angle of the lower palatal lamella (AXP) and for the lip-crest distance (LCD) for each of the populations on which they were measured and the latitude of the sampling locality. As latitude, in turn, is highly correlated with certain specific climatic factors (e.g., TEMPAVE,  $r = -0.974$ ; FFREE,  $r = -0.943$ ; FIRSTKILL,  $r = -0.873$ ; FROST,  $r = 0.845$ ), this suggests the value of looking at total morphology and overall climate by multivariate methods.

### Principal components analysis of morphological structure in extant populations

Principal components analysis of the morphological data, based on the matrix of correlations among the seven variates, was successful in capturing most of the variation among all 339 specimens (those with no missing values for all seven variates) in the first few principal components. Table 5 gives the "loadings," or composition, of each of the first three components in terms of their individual correlation coefficients with each of the original variables. Principal component 1 (PCA1), which accounted for 52.8 percent of the total variation in the data, loaded positively on all variables, especially the height, basal width, and total width of the shell; as is common in morphometric applications of

**Table 3.** Mean values for each locality for the morphometric and climatic variables, and for the scores on the first four principal components. All linear morphometric parameters were measured in hundredths of millimeters. Standard deviations of the morphometric variables are reported below each mean.

Code	H	W	WL	APW	AXP	LCD	BW	LAT	LONG	FROST	TEMPAVE	TEMPJL
A	236.9 12.3	104.4 1.9	5.5 0.2	13.9 1.2	85.3 5.4	16.6 3.1	125.8 3.6	38.26	78.00	9.0	56.0	76.0
B	254.4 12.4	111.1 2.8	5.6 0.3	16.5 1.7	87.3 9.1	18.4 2.8	132.3 5.5	38.57	76.08	8.0	57.0	76.0
C	243.0 14.0	109.3 3.8	5.6 0.3	14.8 0.8	68.5 12.7	16.3 2.5	126.5 4.4	35.97	83.92	9.0	57.5	76.0
D	261.7 9.9	110.1 3.6	5.7 0.3	15.4 1.5	77.3 8.3	14.3 3.1	135.0 4.6	39.10	84.51	9.5	54.5	75.5
E	255.0 9.5	108.9 2.6	5.6 0.2	15.0 1.1	74.8 7.8	14.0 2.8	131.6 3.3	38.38	88.06	10.0	56.0	77.5
F	252.0 11.5	108.0 2.5	5.6 0.3	14.0 1.7	74.1 6.9	14.9 2.4	129.9 4.5	38.62	90.19	15.0	56.0	77.5
G	252.7 9.2	109.7 2.3	5.8 0.3	13.5 1.2	60.9 4.3	18.4 2.8	126.9 3.7	33.27	86.71	2.5	64.0	80.5
H	243.4 5.9	102.4 4.3	5.7 0.2	14.0 1.8	76.1 5.9	16.1 1.7	123.7 5.0	38.91	99.88	16.0	54.0	79.0
I	238.8 13.8	101.7 4.9	5.6 0.3	13.9 2.0	71.7 7.9	15.1 2.6	122.1 6.9	38.91	99.33	16.0	54.0	79.0
J	240.2 10.5	102.3 2.4	5.7 0.2	15.8 1.6	79.0 7.5	16.0 3.1	119.2 3.6	36.73	100.52	10.0	56.0	80.0
K	235.7 10.5	98.3 2.6	5.7 0.3	15.2 0.6	74.3 6.0	18.3 2.5	119.6 4.6	36.73	100.52	10.0	56.0	80.0
L	259.4 14.4	107.7 4.3	5.9 0.3	16.3 1.7	61.9 9.0	20.7 4.0	131.0 6.8	34.85	98.46	7.5	61.5	81.5
M	241.1 15.6	103.9 5.4	5.7 0.3	14.2 1.7	68.2 6.3	15.7 2.6	124.8 6.0	33.60	98.69	6.5	63.0	82.0
N	282.9 17.9	120.2 6.0	6.0 0.3	17.1 1.7	60.9 7.7	25.0 3.9	146.0 6.8	29.95	98.66	2.5	68.0	84.0
O	245.5 10.4	107.8 3.1	5.7 0.3	14.1 1.5	62.0 11.7	18.2 6.2	125.5 3.9	32.34	87.20	2.0	65.5	81.0
P	234.5 6.5	104.1 2.7	5.5 0.2	14.6 1.0	86.6 7.0	18.0 4.6	123.2 3.3	38.89	77.03	11.0	54.0	75.5
Q	225.1 11.5	104.4 2.3	5.2 0.2	79.3 7.9	79.3 7.9	79.3 7.9	79.3 7.9	37.24	76.51	4.0	58.0	77.0
R	243.2 6.2	106.4 2.5	5.3 0.1	73.9 7.4	73.9 7.4	73.9 7.4	73.9 7.4	34.24	77.92	1.5	63.0	79.0
S	247.3 10.5	105.4 2.8	5.5 0.2	72.6 10.2	72.6 10.2	72.6 10.2	72.6 10.2	36.16	86.78	4.5	58.0	78.0
T	233.1 13.5	99.9 3.9	5.3 0.2	81.7 11.7	81.7 11.7	81.7 11.7	81.7 11.7	39.10	94.58	5.0	55.5	78.0
U	236.5 7.0	103.3 2.5	5.4 0.2	79.0 9.1	79.0 9.1	79.0 9.1	79.0 9.1	40.82	96.69	29.0	51.0	77.0
V	230.8 12.0	101.3 3.3	5.3 0.2	80.1 10.1	80.1 10.1	80.1 10.1	80.1 10.1	39.05	95.67	17.5	54.0	77.5
W	252.3 17.6	107.1 4.1	5.5 0.3	74.1 14.4	74.1 14.4	74.1 14.4	74.1 14.4	35.30	99.64	8.0	60.0	81.0
X	275.3 6.5	114.3 3.5	5.6 0.1	63.8 4.3	63.8 4.3	63.8 4.3	63.8 4.3	31.74	99.49	4.0	65.0	83.0
Y	262.0 13.5	110.4 3.8	5.6 0.2	58.2 5.2	58.2 5.2	58.2 5.2	58.2 5.2	35.21	101.83	6.0	57.5	78.0
Z	231.0 10.4	103.6 1.7	5.3 0.3	66.0 7.8	66.0 7.8	66.0 7.8	66.0 7.8	30.29	96.96	1.0	69.0	83.5
AA	237.5 14.3	102.7 3.4	5.4 0.2	70.3 11.8	70.3 11.8	70.3 11.8	70.3 11.8	30.29	96.96	1.0	69.0	83.5
AB	243.8 8.7	107.2 3.7	5.4 0.2	75.3 8.9	75.3 8.9	75.3 8.9	75.3 8.9	31.58	92.52	1.5	67.5	82.5
AC	244.5 11.0	107.1 2.1	5.5 0.3	74.0 8.5	74.0 8.5	74.0 8.5	74.0 8.5	34.73	87.82	3.5	61.0	80.0
AD	243.3 15.7	106.0 5.6	5.4 0.2	78.7 7.5	78.7 7.5	78.7 7.5	78.7 7.5	30.69	88.04	1.0	67.0	81.5
AE	258.6 8.5	107.7 2.6	5.7 0.2	75.8 5.4	75.8 5.4	15.3 2.0	75.8 5.4	39.77	86.16	20.0	52.5	75.0

Table 3. continued

Code	PRECSUM	PRECAVE	FFREE	LASTKILL	FIRSTKILL	CLOUDY	PCA1	PCA2	PCA3	PCA4
A	13.5	40.0	200.0	110.0	298.0	110.0	1.05	-0.70	-0.05	-0.13
B	13.0	40.0	200.0	100.0	307.0	110.0	-0.30	-1.30	0.59	-0.08
C	13.0	50.0	200.0	100.0	295.0	120.0	-0.27	0.41	0.21	-0.46
D	12.0	40.0	180.0	106.0	293.0	135.0	-0.95	-0.64	0.10	0.13
E	10.0	42.0	187.0	105.0	292.0	118.0	-0.45	-0.22	0.25	0.12
F	11.5	40.0	178.0	100.0	292.0	117.0	-0.28	-0.11	0.12	0.06
G	13.0	48.0	220.0	377.0	312.0	110.0	-1.14	0.77	-0.20	-0.33
H	10.0	24.0	170.0	117.0	285.0	75.0	0.41	-0.15	-0.83	0.02
I	10.0	24.0	170.0	117.0	285.0	75.0	0.67	0.37	-0.74	0.01
J	9.5	21.0	190.0	108.0	293.0	65.0	0.64	-0.33	-0.79	-0.08
K	9.5	21.0	190.0	108.0	293.0	65.0	1.03	0.19	-1.34	0.05
L	8.0	30.0	220.0	89.0	303.0	85.0	-1.33	0.58	-0.66	0.01
M	7.0	27.5	220.0	87.0	314.0	88.0	0.17	0.52	-0.65	-0.18
N	7.0	29.0	240.0	79.0	322.0	92.0	-3.55	0.02	0.63	-0.21
O	13.7	48.0	235.0	77.0	316.0	107.0	-0.62	0.84	-0.33	-0.42
P	13.0	40.0	200.0	100.0	103.0	110.0	1.14	-0.81	-0.18	-0.26
Q	16.0	45.0	220.0	95.0	309.0	105.0	1.79	0.17	0.60	-0.25
R	18.0	50.0	240.0	69.0	324.0	90.0	0.63	0.28	0.58	0.20
S	12.0	50.0	200.0	100.0	295.0	125.0	0.25	0.22	0.03	0.21
T	12.0	36.0	182.0	108.0	293.0	102.0	1.75	-0.13	-0.27	0.29
U	11.2	30.0	165.0	119.0	283.0	105.0	1.04	-0.13	-0.17	-0.02
V	12.0	34.0	180.0	112.0	288.0	100.0	1.78	0.06	0.07	0.17
W	8.0	27.0	220.0	95.0	303.0	80.0	-0.11	-0.04	0.16	0.24
X	6.5	25.0	230.0	384.0	314.0	85.0	-2.00	0.33	0.82	0.49
Y	7.0	20.0	180.0	74.0	329.0	55.0	-1.31	1.03	0.32	0.26
Z	8.0	31.0	260.0	79.0	324.0	95.0	1.16	1.15	0.24	-0.06
AA	8.0	31.0	260.0	79.0	324.0	95.0	0.97	0.67	-0.08	0.18
AB	13.0	55.0	240.0	71.0	316.0	105.0	0.42	0.05	0.46	0.03
AC	13.5	52.0	205.0	89.0	303.0	115.0	0.24	0.09	0.26	-0.04
AD	20.0	62.0	280.0	69.0	339.0	98.0	0.63	-0.19	0.31	0.11
AE	11.0	40.0	170.0	115.0	285.0	132.0	-0.61	-0.40	-0.14	0.24

principal components analysis, component 1 can be regarded as a general "size factor." The second principal component (PCA2), accounting for another 15.0 percent of the variation, involved a contrast between both APX, APW and WL (in the sense that loadings on the first two measures were high and negative, while the loading on WL was positive). The third component (PCA3) comprised an additional 11.7 percent of the variation, and consisted of a contrast between, on the one hand, LCD and the angulo-parietal width (APW), and on the other hand, height, the angular measurement (AXP), and whorl height (BW) and shell width (W). Thus, the first three principal components together account for nearly 80 percent of the variation in the morphological structure of *G. procera*, as captured in our seven measurements of 339 specimens from 31 localities across the range of the species.

Inspection of the location of the individual specimens in the three most important dimensions of principal components space (Figure 3) reveals that, as one would expect, the majority of individuals cluster tightly in a central region, corresponding to the average morphology of this snail. However, certain populations consistently deviate from this central tendency. For example, the *G. procera* population from Comfort, TX, clusters at the high end of PCA1, while the *G. procera* population from Dundee, TX clusters at the low end of PCA1 (see Figure 3A, letters N

and M, respectively). Since this component corresponds to a general size factor, snails from Comfort, TX are, on average, the largest in our dataset, while those from Dundee, TX are the smallest (as can be seen from the mean values given for all measurements in Table 3).

The *G. procera* population from Dailsville, MD (letter B) is distinct in lying near the low end of PCA2, corresponding, e.g., to high values of the angular measurement and angulo-parietal width. In contrast, the population from Bear Creek, AL (letter O) at the other extreme of the PCA2 spectrum, has low values for these measures (Table 3).

The plot of PCA2 versus PCA3 (Figure 3B) reiterates the distinctness of the two latter populations (letters B and O), as well as showing a continuum along PCA3 from the Cincinnati, OH population (letter D) at the low end to the Wichita Mountains, OK population (letter L) at the high end. This range corresponds to increasing values of, e.g., the ratio of LCD to height. This is not surprising, given the high correlation between shell height and other size-related parameters (in other words, shell height is an obvious and trivial surrogate for "size") and given the important correlation between LCD and climatic factors such as latitude (Figure 2B).

#### Relationships between multivariate morphological structure and climatic factors

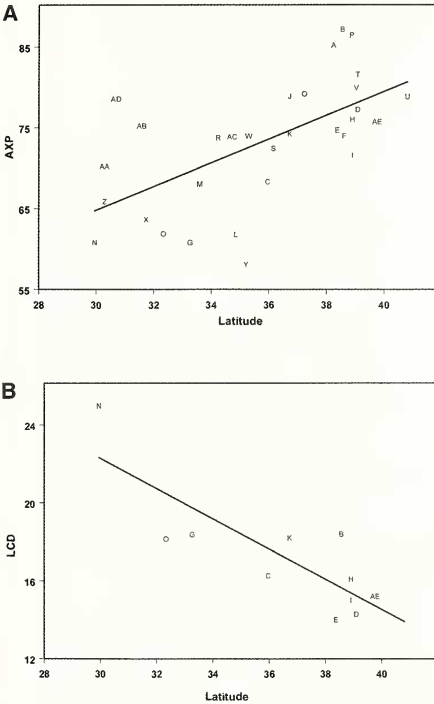


**Table 4.** Pairwise correlation coefficients between morphometric parameters and climatic variables.

	H	W	WL	APW	AXP	LCD	BW
LAT	-0.483	-0.573	-0.771	-0.180	0.843	-0.819	-0.415
LONG	-0.124	-0.387	0.345	-0.161	-0.296	0.209	-0.204
FROST	-0.519	-0.659	-0.579	-0.259	0.594	-0.633	-0.472
TEMPAVE	0.548	0.652	0.744	0.204	-0.774	0.796	0.480
TEMPJUL	0.322	0.214	0.773	0.049	-0.728	0.760	0.207
PRECSUM	-0.374	-0.079	-0.474	-0.395	0.090	-0.391	-0.339
PRECAVE	0.120	0.437	-0.157	-0.140	-0.239	-0.142	0.157
FFREE	0.515	0.665	0.650	0.290	-0.678	0.776	0.475
LASTKILL	-0.051	0.004	0.104	-0.490	-0.342	-0.004	-0.174
FIRSTKILL	0.610	0.727	0.674	0.388	-0.541	0.799	0.565
CLOUDY	0.378	0.559	-0.101	0.133	0.031	-0.251	0.438

**Table 5.** Loadings of the first three principal components (PCA1–PCA3) on the morphometric measurements of *Gastrocopta procera*.

	PCA1	PCA2	PCA3
H	0.48	0.04	-0.28
W	0.45	-0.13	-0.18
WL	0.34	0.31	-0.17
APW	0.30	-0.54	0.27
AXP	-0.21	-0.76	-0.26
LCD	0.30	-0.05	0.82
BW	0.47	-0.12	-0.23
Standard deviation	1.92	1.02	0.90
Percent variance	52.77	14.99	11.67
Cumulative percent variance	52.77	67.76	79.43



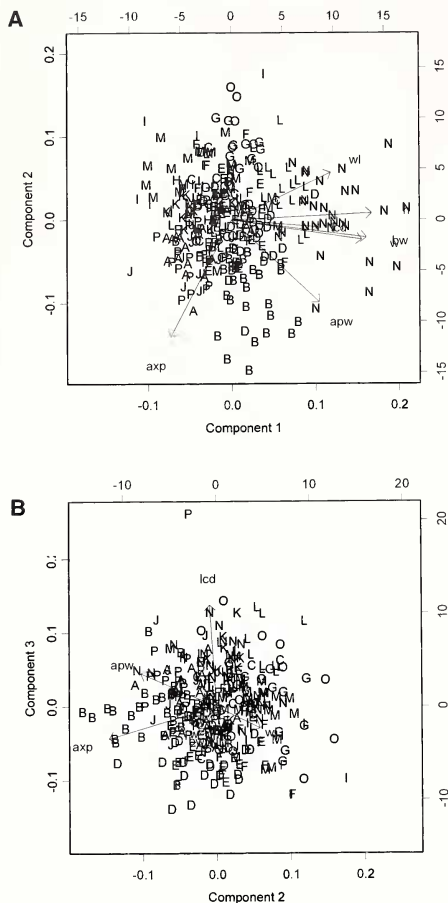
**Figure 2.** Linear regression fits of the two strongest bivariate correlations for *Gastrocopta procera*. A, The increase of AXP, the angle of the lower palatal lamella, with latitude. B, The decrease of LCD, the lip-crest distance, with latitude. Symbols refer to the locality codes of Table 1.

**Table 6.** Correlation coefficients between mean values for the specimens in a locality on each of the first three principal components and the climatic variables.

	PCA1	PCA2	PCA3
LAT	0.3451	-0.5792	-0.3055
LONG	-0.1785	0.4642	-0.4045
FROST	0.1853	-0.3708	-0.3653
TEMPAV	-0.2958	0.5246	0.3547
TEMPJUL	-0.2692	0.5809	0.0160
PRECSUM	0.3965	-0.3052	0.2470
PRECAVE	0.1079	-0.1426	0.4463
FFREE	-0.1059	0.3636	0.3835
LASTKILL	-0.3206	0.1254	0.0834
FIRSTKILL	-0.2417	0.4382	0.2333
CLOUDY	-0.0027	-0.3624	0.3578

Table 6 gives the correlations between the mean values for each locality of each of the first three principal components and the values for each of the 11 climatic factors for each locality. It is clear, for example, that PCA1 is positively correlated most highly with total precipitation ( $r = 0.397$ ) and with latitude ( $r = 0.345$ ) and negatively correlated most highly with the date of the last killing spring frost ( $r = -0.321$ ) and with average annual temperature ( $r = -0.296$ ). This suggests that the general size of the shell of *G. procera* (PCA1) will be larger (and therefore the organism will attain larger sizes) at higher latitudes, which are typically colder and wetter within the continental United States. In this respect, *G. procera* appears to follow Bergman's rule.

The second principal component is most strongly positively correlated with the annual average and the midsummer temperature ( $r = 0.525$  and  $r = 0.581$ , respectively) and negatively correlated ( $r = -0.579$ ) with latitude (Table 6). Since higher latitudes correspond with lower temperatures over the biogeographic range of *G. procera*, these relationships imply that, based on our interpretation of PCA2 as determined primarily by a contrast between measurements of the aperture (APW and AXP) and WL,



**Figure 3.** Location of specimens belonging to various populations of *Gastrocopta procera* (indicated with the locality codes of Table 1) in the morphometric space defined by the first three principal components based on the seven measurements of Table 2.

snails belonging to this species exhibit a relationship between climatic factors and functional morphology of the aperture that is not explained by general size alone.

The third principal component is positively correlated with average annual precipitation ( $r = 0.446$ ) and negative-

**Table 7.** Results of multiple stepwise linear regression of the first two principal component of morphometric variables for *Gastrocopta procera* (PCA1) on the climatic variables.

Coefficients for PCA1:				
	Value	Std. error	t-value	Prob.(>  t )
(Intercept)	-41.0362	10.7264	-3.8257	0.0007
LAT	0.5889	0.1642	3.5874	0.0014
LONG	0.0830	0.0322	2.5773	0.0160
PRECSUM	0.1531	0.0822	1.8633	0.0738
FFREE	0.0519	0.0176	2.9459	0.0067

Residual standard error: 0.9107 on 26 degrees of freedom

Multiple R-squared: 0.4823

F-statistic: 6.056 on 4 and 26 degrees of freedom (P-value is 0.001394)

Coefficients for PCA2:				
	Value	Std. error	t-value	Prob.(>  t )
(Intercept)	3.2880	5.2289	0.6288	0.5348
LONG	0.0568	0.0207	2.7495	0.0105
TEMPAVE	0.1268	0.0498	2.5439	0.0170
TEMPJL	0.2009	0.1217	-1.6507	0.1104

Residual standard error: 0.4107 on 27 degrees of freedom

Multiple R-squared: 0.4850

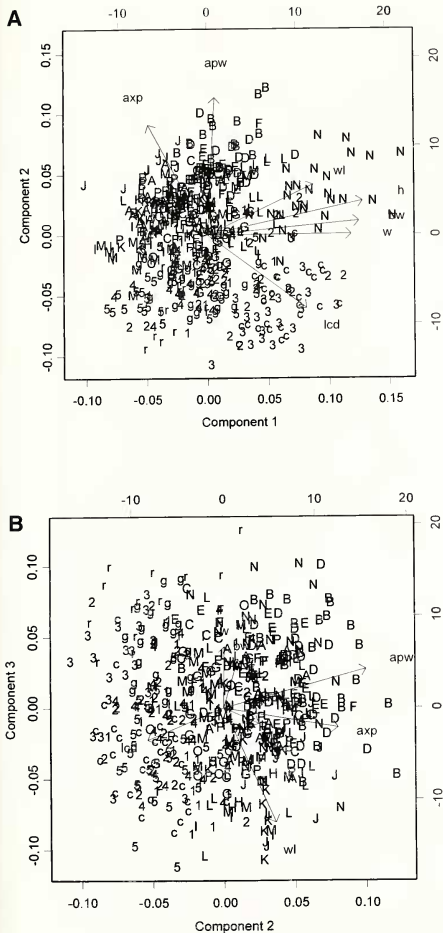
F-statistic: 8.475 on 3 and 27 degrees of freedom (P-value is < 0.001)

ly correlated with longitude ( $r = -0.405$ ). Our interpretation of PCA3 as a structural factor related to the relative size of the lip-crest distance (LCD) compared with the height of the shell suggests that snails with relatively large LCD are more likely to be found under the wetter conditions that are commonly found in the eastern part of the range of *G. procera*.

These and other piecemeal interpretations of the relationships between morphological structure and general climatic factors are intriguing. However, a more satisfactory approach is to find the best fit between values of morphological factors (in our case, principal components) and the entire set of climatic variables. Table 7 gives the results of the best multilinear regressions between each of the first three principal components and the 11 climatic variables. Thus, PCA1 is fit very well (multiple  $R$ -squared =  $-0.482$ ,  $P < 0.01$ ) by a linear combination of latitude, longitude, total annual precipitation, and number of frost-free days, with the highest loadings on latitude and number of frost-free days. In other words, these four climatic variables have a highly significant predictive value for the major axis of morphological variation in extant populations of *G. procera*, an axis that accounts for more than half of the structural variation among 339 specimens sampled from 31 extant populations across the biogeographic range of the species.

Similarly, PCA2, the next most important general morphological factor can be predicted quite well (multiple  $R$ -squared =  $0.485$ ,  $P < 0.001$ ) by a linear combination of longitude and the two measures of average temperature (positively with respect to TEMPAVE for annual and negatively with respect to TEMPJL for July).





**Figure 4.** Location of specimens belonging to various populations of four species of *Gastrocopta* (indicated with the locality codes of Table 1) in the morphometric space defined by the first three principal components based on the seven measurements of Table 2. Populations of Holocene *G. procera* are denoted with uppercase letters; Pliocene *G. franzenae* populations are indicated with numerals; two Holocene *G. riograndensis* populations are denoted with the lowercase letter “r” and “g”, while a single Holocene population of *G. cristata* is denoted with the lowercase letter “c”

**Table 8.** Loadings of the first three principal components on the morphometric measurements of four *Gastrocopta* species.

	PCA1	PCA2	PCA3
H	0.51	0.17	-0.10
W	0.47	0.01	0.41
WL	0.35	0.25	-0.76
APW	0.02	0.68	0.26
APX	-0.20	0.55	-0.13
LCD	0.33	-0.37	-0.21
BW	0.50	0.07	0.33
Standard deviation	1.83	1.21	0.87
Percent variance	47.71	20.97	10.88
Cumulative percent variance	47.71	68.68	79.56

### Morphological structure of fossil and congeneric populations

Data for 141 specimens belonging to five populations presumed to belong to the paleospecies *G. franzenae*, as well as 37 specimens from two populations of the Holocene species *G. riograndensis* and 29 specimens from one population of the Holocene species *G. cristata*, were combined with the 339 specimens of *G. procera* in a separate analysis. Figure 4 shows the disposition of both the fossil and extant specimens in the first three dimensions of *Gastrocopta* morphological space, and Table 8 gives the composition of the first three principal components, which together account for 80 percent of the total variation in the dataset of 546 *Gastrocopta* specimens. What is evident is that, while some of the fossil populations (e.g., population 4, from Seward County, KS) correspond to the size and shape of typical extant populations, some (population 5, from Meade County, KS) are located at the low end and some (population 3, from Oldham County, TX) are located at the high end of PCA1, which accounts for 48 percent of the total morphological variation. Since PCA1 again can be interpreted as a general size factor (although this time negatively correlated with the angular dimension), this implies that the fossil populations span the same range of sizes as modern populations.

Even more interesting, most of the fossil populations, as well as the other two extant species, lie at one end of the spectrum along PCA2 (Figure 4A), while none are located at the other end of this spectrum. PCA2 is primarily a contrast between APW and APX, on the one hand, and LCD, on the other (Table 8). This might be interpreted as a shift over evolutionary time in this organism from populations of snails with primarily one form of aperture morphology to the more typical morphology seen at the present time. However, since we have data only for a few fossil populations from one particular geographic region, such a conclusion is premature at this time.

What is most clear from the principal component analysis of all four *Gastrocopta* species is that the fossil species, *G. franzenae*, lies at one end of the morphological spectrum, in an area that overlaps with *G. riograndensis* and *G. cristata*, as well as some populations of *G. procera*. This supports the possibility that the evolution of morphological structure in this gastropod genus has been unidirectional over time, and that that direction is partially captured by PCA2. If so, *G. riograndensis* and *G. cristata* are more primitive than *G. procera*. This view would be strengthened by analyses of additional populations of fossil and extant species.

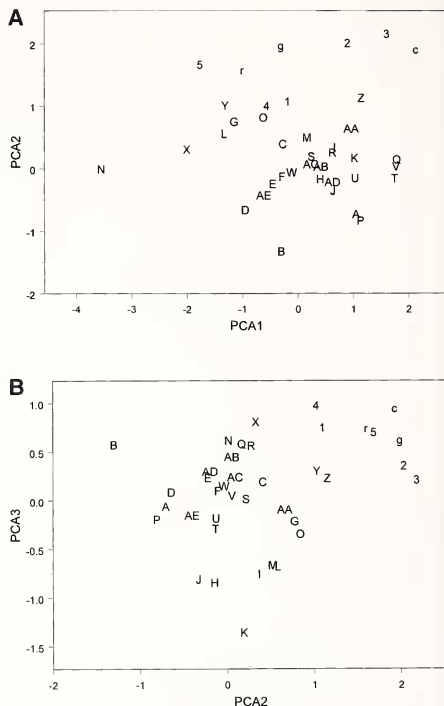
*Gastrocopta riograndensis* appears to occur in one restricted region of the morphological space defined by the first three principal components, while *G. cristata* lies in a different corner; the presumed ancestral species, *G. franzenae*, spans this region. However, only two populations of the first and one of the latter species were sampled, so this conclusion is tantalizing but not definitive. Clearly, more work on the systematics of these species is warranted.

#### Predicted climatic conditions for fossil populations

What the morphological distinctness of several of the fossil populations can tell us with some certainty are inferences about possible climatic conditions that were present at the time that the fossil populations were alive. These inferences rely on the assumption that the fossil populations belong either to the same biological cluster of species as the living ones (continuity of descent) or to species sufficiently similar in biology that they respond in the same way to major environmental factors.

Our results suggest that we may use the location of fossil populations in morphological space and the relationships between extant morphology and modern climatic conditions to predict aspects of paleoclimatic conditions. In particular, the location of the fossil populations at the high end of PCA2 (Figure 5) strongly suggests that they lived in conditions similar to those now present in the southern parts of the range of *G. procera*, corresponding to populations Y, Z, AA, and O (from Texas and Alabama; see Table 1). Unfortunately, there are no climatic inference data for the specific fossil localities sampled.

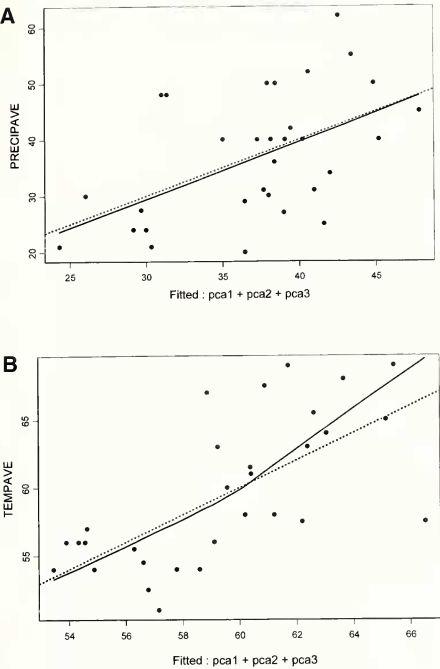
The correspondence between shell structural parameters and climatic variables can be used to predict the values of major climatic variables from the morphological principal components, using regression analysis. For example, Figure 6 and Table 9 illustrate the very good predictive ability of the first three principal components of morphology from *G. procera* in predicting the average annual temperature (TEMPAVE) and the average annual precipitation (PRECAVE) of the locations from which the populations were sampled. Assuming that we are correct in regarding all *Gastrocopta* species as responding,



**Figure 5.** Location of the population means of all four species of *Gastrocopta* in the morphometric space defined by Holocene *G. procera* populations, as given in Figure 3. Abbreviations are as in Table 1 and Figure 4.

in their shell morphology, similarly to long-term climatic conditions, we can use these strong linear relationships in extant populations to predict plausible climatic conditions for the fossil populations of *G. franzenae*, *G. riograndensis*, and *G. cristata*. Table 10 gives the predicted values for these populations for these two variables, along with their 95 percent confidence limits. These results suggest, for example, that populations of the putative ancestral fossil species, *G. franzenae*, may have lived under conditions even warmer and wetter than those of present-day populations of the descendant species, *G. procera*, from Texas and Alabama.

These inferences from our morphological analyses could be tested further by more direct analyses of paleoclimate information for the fossil strata from which *G.*



**Figure 6.** Predictions of average annual precipitation (A) and average annual temperature (B) based on the first three principal components of morphological structure in *Gastrocopta procera*. The dotted lines are the best linear regression fits, while the solid lines are the best polynomial fits.

*franzeneae* was sampled. The general approach of this paper illustrates the potential value of using morphology in the reconstruction of paleoclimatic conditions when other data might be unavailable.

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**Table 9.** Regression coefficients for predicting average annual precipitation (PRECAVE) and average annual temperature (TEMPAVE) from the first three principal components of morphological structure in *Gastrocopta procera*.

Coefficients for PRECAVE:				
	Value	Std. error	t-value	Pr(>  t )
(Intercept)	37.3323	1.8593	20.0782	0.0000
PCA1	2.2548	1.6589	1.3592	0.1853
PCA2	-1.4768	3.4748	-0.4250	0.6742
PCA3	11.2385	3.8549	2.9154	0.0071
Residual standard error: 10.17 on 27 degrees of freedom				
Multiple R-squared: 0.2611				
F-statistic: 3.18 on 3 and 27 degrees of freedom (P-value is 0.03993 )				
Coefficients for TEMPAVE:				
	Value	Std. error	t-value	Pr(>  t )
(Intercept)	59.0760	0.7627	77.4578	0.0000
PCA1	-0.5801	0.6805	-0.8525	0.4014
PCA2	5.2831	1.4253	3.7066	0.0010
PCA3	3.8412	1.5812	2.4292	0.0221
Residual standard error: 4.173 on 27 degrees of freedom				
Multiple R-squared: 0.449				
F-statistic: 7.333 on 3 and 27 degrees of freedom (P-value is < 0.001 )				

**Table 10.** Predicted average annual precipitation (PRECAVE) and average annual temperature (TEMPAVE), and their standard deviations (Std.) and 95 percent confidence limits, for Pliocene populations of *Gastrocopta franzeneae* (codes 1–5), and Holocene populations of *G. riograndensis* (codes r and g) and *G. cristata* (code c).

PRECAVE:				
Code	Inches	Std.	Lower	Upper
1	43.90	5.14	43.90	52.66
2	40.56	7.74	27.37	53.74
3	40.31	8.52	25.79	54.83
4	45.72	5.49	36.37	55.08
5	38.93	6.74	27.44	50.41
r	41.22	6.42	30.29	52.15
g	40.89	7.48	28.15	53.63
c	50.14	9.52	33.92	66.35
TEMPAV:				
Code	°F	Std.	Lower	Upper
1	67.92	2.11	64.33	71.51
2	70.72	3.18	65.31	76.13
3	70.54	3.50	64.58	76.49
4	68.65	2.25	64.81	72.49
5	71.77	2.77	67.06	76.49
r	71.03	2.63	66.54	75.51
g	72.22	3.07	67.00	77.45
c	71.74	3.91	65.09	78.39

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